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The compass within

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Abstract

Head direction cells have been hypothesized to form representations of an animal's spatial orientation through internal network interactions. New data from mice show the predicted signatures of these internal dynamics.

Have you ever stepped out of the elevator in an office building or hotel and turned down the hallway only to realize that you had turned the wrong way and were headed in the wrong direction? In that moment when something didn't seem right, did the world seem to spin around you as you reoriented to your intended heading? This internal sense of orientation occurs because there are cells in several brain areas that maintain a cognitive representation of your heading. These so-called head direction cells, along with other cells that represent particular locations in an environment, make it possible to know where we are and how to get where we are going. Head direction cells have been hypothesized to maintain a representation of orientation through internal network dynamics, and in an elegant study examining head direction ensembles in mice, Peyrache *et al.*¹ directly reveal these internal network dynamics.

Head direction cells were first reported in a Society for Neuroscience abstract by Ranck in 1984 (Ranck, J.B. Jr., *Soc. Neurosci. Abstr.* **10:599**, 1984), and the first thorough description of them was made by Taube *et al.*² in 1990. Head direction cells are found in a number of structures, including the anterior dorsal nucleus of the thalamus (ADN), the postsubiculum (PoS) and the lateral mammillary nuclei^{3,4}. A typical head direction cell shows a tight, monotonic tuning to a particular direction, and, as a group, they are thought to represent orientation by the subset of cells that are active at any given time⁵.

In the mid-1990s, theoreticians suggested that a mathematical model called an attractor network (now known as a ring attractor) could explain how interactions between head direction cells could generate their directional tuning properties and how the directional representation of heading could be continuously maintained across changing orientations by coherent shifts in the functional interactions in head direction networks^{5–8}. This theoretical framework predicted an internal generation of the sense of orientation and explained how sensory cues could keep the representation aligned with the world or could bring it back into register when disoriented^{2–5,9–12}.

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The ring attractor theory proposed that head direction cells that represent nearby directions (with similar tuning curves) would be positively coupled, whereas cells tuned to distal orientations would be negatively coupled^{5–8}. This pattern of functional connectivity, local excitation amidst global inhibition, generates a bump or packet of activity. The theory implies that the activity packet should be coherent even in the absence of external input (Fig. 1)^{5,8,13,14}. The location of the activity packet on the representational ring differentiates one heading from another^{5–8}. This internal generation of a heading percept therefore represents a cognitive sense, much like an internal ‘neural compass’ in which the compass needle corresponds to the packet of active neurons that generate the heading representation. Unlike a compass, which detects an external magnetic field, the head direction system defines its own internal north. Notably, the ring attractor theory predicts that internal neural coordination of the head direction signal is primary^{5–9} and that environmental information could become associated with the internal sense to guide navigation^{9–12}.

The predictions of the ring attractor theory could only be tested with sufficiently large simultaneously recorded neural ensembles. To reveal these attractor dynamics in terms of the functional interactions between neurons, Peyrache *et al.*¹ recorded ensembles of head direction cells from two brain areas, the ADN and the PoS. Notably, pairs of neurons with more similar head direction preferences showed strongly correlated activity in terms of both spike rates and timing, and neuron pairs with very different directional preferences showed negatively correlated activity. Peyrache *et al.*¹ found that the pairwise correlations between head direction cells transitioned from positive to negative correlations at 60 degrees of angular offset, linking the underlying functional network connectivity to the parameters of the tuning curves of individual head direction cells.

The ring attractor theory also predicted that the activity packet across the ring attractor should be coherent and self-consistent, even in the absence of external inputs. Peyrache *et al.*¹ evaluated head direction ensemble activity during waking and sleep states, finding coherent, but drifting, representations (what they call the virtual gaze) during sleep. This is clear evidence that functional connectivity in head direction networks is capable of continuously representing adjacent headings in terms of functionally adjacent (overlapping) network states and that the network states that represent different directions are robust across brain states. During slow wave sleep, this coherent representational drift was maintained at a much faster timescale than during waking or REM sleep, which is reminiscent of the temporal compression of hippocampal sequence replay events during slow-wave sleep¹⁵. Whether the drift in head direction representation during sleep corresponds to any other representations that replay during sleep (such as in hippocampus and neocortex) is a very intriguing, but open, question.

Both of the brain structures that Peyrache *et al.*¹ recorded from exhibited dynamics consistent with attractor theory, but the coordinated activity in ADN exhibited stronger internal coherence than that in PoS. Furthermore, the correlations between ADN-PoS neuron pairs were stronger than the correlations between PoS-PoS neuron pairs. Other researchers have suggested that the ring attractor that underlies the head direction representation occurs upstream of ADN and PoS and is passed down to them³. The data from Peyrache *et al.*¹ suggest that the head direction information is passed down from ADN to PoS, but suggest

that ADN or its upstream inputs do contain the ring attractor dynamics to generate the internal sense of direction. Further causal manipulations will be required to determine exactly which brain structures internally generate the head direction signal.

The importance of the findings presented by Peyrache *et al.*¹ is that their observation of coherent representations during both waking and sleep states implies an internally generated head direction representation. Their data support the well-developed theory of attractor-based internal generation of the orientation sense in the head direction system. The attractor network framework provides a clear context in which many already established findings regarding the head direction system have been understood. Sometimes, theory suggests incisive experiments that yield results that force us, as researchers, to re-orient the trajectory of our inquiries. In this case, the elegant findings presented by Peyrache *et al.*¹ embody a striking confirmation that these theories have headed us in the right direction.

References

1. Peyrache A, Lacroix MM, Perersen P, Buzsáki G. Nat. Neurosci. 2015; 18:569–575. [PubMed: 25730672]
2. Taube JS, Muller RU, Ranck JB Jr. J. Neurosci. 1990; 10:420–435. [PubMed: 2303851]
3. Taube JS, Goodridge JP, Golob EJ, Dudchenko PA, Stackman RW. Brain Res. Bull. 1996; 40:477–484. [PubMed: 8886377]
4. Sharp PE, Blair HT, Cho J. Trends Neurosci. 2001; 24:289–294. [PubMed: 11311382]
5. Redish, AD. Beyond the Cognitive Map. MIT Press; 1999.
6. Skaggs, WE.; Knierim, JJ.; Kudrimoti, HS.; McNaughton, BL. Advances in Neural Information Processing Systems. MIT Press; 1995. p. 173-180.
7. Redish AD, Elga AN, Touretzky DS. Network: Computation in Neural Systems. 1996; 7:671–685.
8. Zhang K. J. Neurosci. 1996; 16:2112–2126. [PubMed: 8604055]
9. Knierim JJ, Kudrimoti HS, McNaughton BL. J. Neurosci. 1995; 15:1648–1659. [PubMed: 7891125]
10. Goodridge JP, Taube JS. Behav. Neurosci. 1995; 109:49–61. [PubMed: 7734080]
11. Taube JS, Burton HL. J. Neurophysiol. 1995; 74:1953–1971. [PubMed: 8592189]
12. Blair HT, Lipscomb BW, Sharp PE. J. Neurophysiol. 1997; 78:145–159. [PubMed: 9242269]
13. Wilson HR, Cowan JD. Kybernetik. 1973; 13:55–80. [PubMed: 4767470]
14. Amari S. Biol. Cybern. 1977; 27:77–87. [PubMed: 911931]
15. Nádasdy Z, Hirase H, Czurko A, Csicsvari J, Buzsaki G. J. Neurosci. 1999; 19:9497–9507. [PubMed: 10531452]

Figure 1.

The attractor-network model of the head direction system produces a coherent head direction representation even in the absence of external inputs. **(a)** The ring attractor network. Each cell is positively coupled (blue) to its representational neighbors and negatively coupled (red) to the entire ring, which produces a structure of local excitation amidst global inhibition. **(b)** Even in the absence of external inputs, the internal dynamics of the ring network settles to a ‘bump’ or ‘activity packet’ (red, high activity; blue, low activity). This specific simulation was generated using code from ref. 5, but all ring attractor models produce equivalent dynamics. **(c)** An activity packet seen by Peyrache *et al.*¹ during sleep states, showing the ‘virtual gaze’ of the mouse (reprinted from ref. 1 with permission).